Fokker-Planck model for movement of the carabid beetle *Pterostichus melanarius* in arable land: Model selection and parameterization

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Carabid beetles in arable land move between different habitats to exploit resources that vary in time and space. Understanding such movement is key to explaining how the pest control function of carabids in arable crop lands depends on the spatial configuration of crop fields and associated semi-natural habitats, but movement at and beyond field scale is not well understood. Here we use a model selection framework to identify and parameterize a parsimonious movement model, based on mark-release-recapture data in two adjacent arable crop fields, one planted with rye, and the other with oil radish. The simplest model assumes motility of beetles to be the same in the two crops, and it does not consider losses of beetles over time due to death or mark loss. These assumptions are relaxed either separately or together in competing models, resulting in a comparison between four models. All models consider the effect of spatially heterogeneous pitfall trapping on the size of the moving population. Models were fitted to data with Poisson likelihood, and Akaike's information criterion was then used to rank the models. The model selection showed that including a parameter for loss of beetles due to mortality or mark loss resulted in the best approximation of the observed data. The data did not support the assumption of different motility between the two crops. We conclude that our extended model can be used to simulate beetle recapture in mark-release-recapture experiments, but further refinements to the model are needed. The inverse modeling framework for model identification and parameter estimation that was applied in this study proved effective to select the most promising model and parameter values.

Keywords: Pterostichus melanarius, dispersal, Poisson distribution, AIC, model selection

In mark-release-recapture (MRR) experiments, a large number of insects are released into an area and recaptured over time. Data from this type of experiments either consist of dispersal distances or the locations and time at which a certain number of beetles is recaptured (Turchin 1998). Analysis of these data can provide insight in insect population dispersal patterns. A common way to analyse such MRR data is to consider animal population spread as a continuous diffusion process (Inoue 1978, Kareiva 1982, Turchin 1998, Cronin *et al.* 2000, Yamamura 2002, Reeve *et al.* 2008). Diffusion in one or more dimensions is described by partial differential equations (PDEs). According to Yamamura *et al.* (2002), one advantage of PDEs is their mathematical tractability, *i.e.* there are analytical solutions available that describe animal density in time and space. Unfortunately, analytical solutions of these models cannot take spatially heterogeneous removal by recapture into account. If a substantial part of the beetle population is removed in the course of the experiment, the process of beetle removal by catch must be accounted for. Fagan (1997) presented an experimental approach to do this. He conducted a MRR experiment in which he released mantids and recaptured them at the boundaries of the experimental field. He used a diffusion model to analyse his data assuming absorbing boundaries. This approach, however, cannot be applied to analyse MRR data that consist of counts of insects that are recaptured within the experimental field. Yamamura *et al.* (2003) solved this problem by adding a loss term to the diffusion equation for beetle removal due to catching. Their model, however, requires that traps are placed uniformly in a lattice pattern.

Usually, PDE-based movement models for insects are based on Fickian diffusion. However, as pointed out by Turchin (1998), ecological diffusion should be based on the Fokker-Planck equation. The distinction is important because the Fokker-Planck equation results in a non-homogeneous steady state, where local density is inversely proportional to motility, whereas ordinary Fickian diffusion demonstrates continuous dissipating density gradients until the density has become spatially homogeneous.

Here, we present a movement model that accounts for local removal due to catching that can be applied for any spatial configuration of traps. Dispersal in this model is based on the Fokker-Planck equation. We identified the model using data from an MRR experiment with the common carabid beetle *Pterostichus melanarius* Illiger in arable land. We wanted to know if, besides removal due to trapping, also a removal term should be included in the model for mortality and mark wear, and secondly, we wanted to know if a different motility should be implemented for two fields grown with different crop species. We formulated four Fokker-Planck models to answer these questions: (1) without mortality and without a crop specific motility; (2) with mortality and without a crop specific motility; (3) without mortality and with a crop specific motility; and (4) with mortality and with a crop specific motility. In all these models

mortality includes mark wear. Model selection was used to rank models and select those with the greatest support from the data (Hilborn & Mangel 1997, Bolker 2008). Ranking was based on Akaike's information criterion (Akaike 1974, van der Hoeven *et al.* 2005).

MATERIAL AND METHODS

Field experiment

A mark-release-recapture experiment with *P. melanarius* was performed on parcel 5 of the organic university farm Droevendaal (Wageningen, The Netherlands) in 2009. The parcel measured 229 × 52 m² and was bordered at all sides by a 3-6 m wide grass margin and at the north side by a grass margin with a hedgerow of 1.5-2.5 m tall shrubs. The MRR experiment was carried out in a 120 × 52 m study area within this parcel. One half of the area was grown with winter rye (*Secale cereale* var. Admiraal) and the other half with oil radish (*Raphanus sativus* var. Brutus). Both crops were sown in the first week of August 2009 to a row spacing of 12.5 cm.

The beetles were released on 7 September 2009 at 6 p.m. (1015 in oil radish and 1015 in winter rye) along a 12-m-long line in both crops (Figure 1). Beetles released in winter rye were marked with gold nail polish (OPI Nail lacquer, NL H41) while beetles released in oil radish were marked with pink nail polish (OPI Nail lacquer, NL B777). Trapping stations (Ø 8.5 cm) were placed in parallel lines at 10, 20 and 30 m from the release lines. The released beetles had been collected by pitfall trapping in a triticale field on the same farm during summer. Beetles were sexed and only females were retained. They were stored in 300 × 400 mm containers in a dark room at 4 °C until the time of release. Beetles were

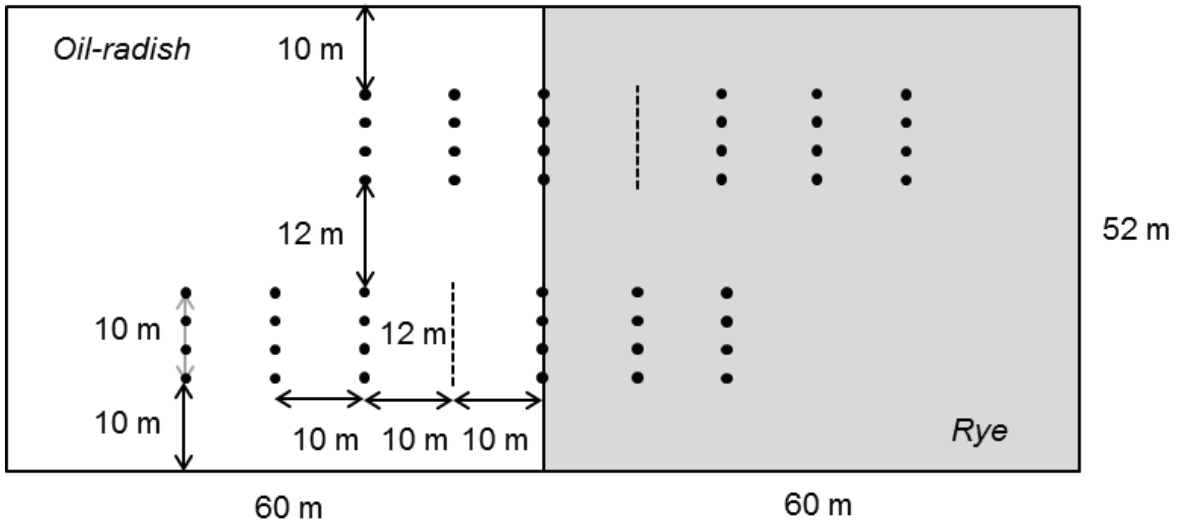

Figure 1. The set-up of the mark-release-recapture experiment with oil radish (left) and winter rye (right). Dots indicate the trap positions. Dashed lines indicate the beetle release lines.

fed with fly maggots (*Lucillia caesar*) during storage. The mark was applied a few days before release. A plastic screen of 1.40 m was placed behind (as seen from the release site) the traps at 20 and 30 m from the release line to increase trapping probability. The trapping stations were emptied to count recaptured beetles between September 8 and September 30, 2009, with an interval between catches of 1, 2 or 3 days. Recaptured beetles were not returned to the field.

Model development

We compare four movement models. We simulated beetle dispersal according to the Fokker-Planck equation and included a term for the fraction of beetles that was trapped per unit of time because a substantial part of the marked beetles was captured (in total 468 pink and 528 gold beetles). A loss rate was also included because marked beetles could die, or more likely, loose their mark over time. The PDE of the most complicated model (our model 4, see below) is given in equation 1. The other three PDEs are simplified versions of equation 1.

$$\frac{\partial N(x,y,t)}{\partial t} = \frac{\partial^2 \mu(x,y) N(x,y,t)}{\partial x^2} + \frac{\partial^2 \mu(x,y) N(x,y,t)}{\partial y^2} - [\alpha(x,y) + \xi]\, N(x,y,t) \qquad (1)$$

for $x \leq 60$ it holds that $\mu(x,y) = \mu_1$ and for $x > 60$ it holds that $\mu(x,y) = \mu_2$.

Here, $N(x,y,t)$ is the number of beetles at location (x,y) at time t, μ_1 is the motility ($m^2\ day^{-1}$) in oil radish, μ_2 the motility in winter rye, ξ (day^{-1}) is the loss rate due to mark wear and mortality and $\alpha(x,y)$ (day^{-1}) is the loss rate due to recapture at location (x, y). Our simplest model, model 1 describes beetle dispersal with local recapture: $\mu_1 = \mu_2$ and $\xi = 0$. In model 2 the basic model is extended with spatial independent loss rate: $\mu_1 = \mu_2$ and $\xi \neq 0$. In model 3 the basic model is extended with a habitat specific motility: $\mu_1 \neq \mu_2$ and $\xi = 0$. Finally, in model 4 the basic model is expanded with both the loss rate and a habitat specific motility: $\mu_1 \neq \mu_2$ and $\xi \neq 0$. For the catch we estimated the global catch efficiency ω with $\alpha(x,y) \equiv \phi\omega\, \mu(x,y)/\Delta x \Delta y$, with $\phi = 1$ at the location of the trap and $\phi = 0$ at all other locations.

In order to simulate beetle dispersal in time and space, boundary conditions and initial conditions have to be formulated. In the field experiment beetles were released on a 12 m transect in winter rye and oil radish. In the model it is assumed that the beetles were released from four equally spaced points on these release lines.

Several boundary conditions were compared. Reflecting boundaries are not appropriate because they do not allow beetles to leave the field, which they can do in reality. On the other hand, zero boundary conditions are neither appropriate, because they would allow beetles to leave the field, never to return, resulting in an overestimation in beetle losses from the field. We explored model

behaviour for different boundary conditions and found that a 'slow release boundary' around the field gave the most satisfactory and credible simulation results. The slow-release boundary consists of a 1-m-wide strip around the field with a low motility (μ_3). This low motility results in an aggregation of beetles in this margin, and a slow release back to the field from this boundary. The value of μ_3 was determined once by optimisation for the least restricted model (Eq. 1) and then used as a constant for the optimization of the other models. Optimisation was based on the Poisson negative log-likelihood (see below) and resulted in a value of μ_3 of 3 m^2 day^{-1}.

Numerical approximation

None of the four considered models can be solved analytically, because ϕ is spatially heterogeneous. Consequently, numerical approximations are required in order to run simulations and analyse the field data. The PDEs were solved numerically by the forward central difference method.

Estimation of the parameters

The most suitable model and the value of model parameters were identified using an inverse modelling approach employing the evolutionary algorithm of Differential Evolution (Storn & Price 1997). The Poisson negative log likelihood (NLL) was used as a measure for goodness of fit. This measure was calculated as follows:

$$\mathrm{NLL} = \sum_x \sum_y \sum_t \left\{ N_{\mathrm{predicted}}(x,y,t) - N_{\mathrm{data}}(x,y,t) \ln[N_{\mathrm{predicted}}(x,y,t)] + \ln[N_{\mathrm{data}}(x,y,t)!] \right\} \quad (2)$$

Here, $N_{\mathrm{data}}(x,y,t)$ represents the number of trapped beetles in the field experiment at a given time and location, $N_{\mathrm{predicted}}(x,y,t)$ represents the number of trapped beetles at a certain time predicted by the model corresponding to the chosen model (with or without habitat specific movement).

Model selection

Based on the number of estimated parameters p and the NLL, models can be compared by using Akaike's information criterion (Akaike 1974, van der Hoeven *et al.* 2005, Hilborn & Mangel 1997):

$$\mathrm{AIC}_i = 2\mathrm{NLL}_i + 2p_i \quad (3)$$

Here, i is the index of the model (i = 1...4). The AIC considers all models with $\Delta\mathrm{AIC} < 2$ equivalent. For model validity also AIC-weights can be calculated within the set of four models considered. Here the AIC weight for model i (with i = 1...4) is:

$$\mathrm{AIC\,weight}_i = \frac{\exp(-\Delta\mathrm{AIC}_i)}{\sum_{i=1}^{4} \exp(-\Delta\mathrm{AIC}_i)} \quad (4)$$

RESULTS

Comparison of models with Akaike's information criterion demonstrated that models with beetle losses (models 2 and 4) were far superior over those without losses, the former having AIC values that were approximately 238 smaller than the latter (Table 1). The better fit of models with beetle losses is graphically illustrated in Figure 2. According to the criterion that models differ if their AIC-values differ more than 2 we can conclude that no difference exists between models 2 and 4. This is confirmed by the AIC weights of 0.66 for model 2 and 0.34 for model 4, indicating support for both models. Nevertheless, the AIC weights of models 2 and 4 show that model 2 which has a single parameter for the motility is more likely to explain the observations in the field experiment than model 4 which has crop-specific parameters for motility.

DISCUSSION AND CONCLUSIONS

The results convincingly show that loss of beetles should be accounted for in the model describing dispersal. We have also shown that the *P. melanarius* population dispersal in the field experiment is more likely to be similar across crop habitats than habitat specific.

The model could be made more specific by accounting for the plastic screens that were placed behind the traps at 20 and 30 m (but not at 10 m) to increase catching rate. This can be achieved by assigning different parameter values for trap locations with or without a screen. The model could also be expanded with the addition of the grass margin at the northern side and the grass margin without hedgerow at the southern side of the simulated field. The disadvantage of this addition is that there are no recapture data from these habitats and that the motility in that border can only be estimated indirectly from data collected in oil radish and winter rye.

Although the speed of beetles' dispersal seems not to be affected by different habitat types, it does not necessarily mean that beetles do not have a preference for one of the crop types. In further research, it could be investigated whether beetle dispersal is influenced by the interface between two habitat types, rather than by the habitat type itself. This approach may provide more insight in whether beetles are attracted or repelled by a habitat type if they approach the interface between different habitat types.

One disadvantage of MRR experiments is that recapturing beetles dilutes the population density in the field by preventing further dispersal of beetles once they are recaptured. In the 'boundary flux approach' designed by Fagan (1997), reaction-diffusion models are used to analyse beetle dispersal by considering recapturing at the edge of the experimental field. This approach makes it no longer necessary to account for beetle population density dilution by recapturing beetles in the field. However, this type of experiment does not allow using data from traps within the experimental field and indirectly estimates beetle densi-

Table 1. Results of the model selection for the four Fokker-Planck models describing beetle dispersal in two crops, arranged by increasing AIC; Model: model number as explained in text; p: number of estimated parameters in the model. Model parameters: ξ: loss rate; μ_1 and μ_2: motility in oil radish and winter rye crops (if $\mu_1 = \mu_2$ then the value is put in the middle); ω: dimensionless global catch efficiency of the traps; AIC: Akaike's information criterion; ΔAIC: difference in AIC with the best model; AIC weight: a measure of belief in the current model (out of the considered four models).

Model	p	ξ (day^{-1})	μ_1 (m^2 day^{-1})	μ_2 (m^2 day^{-1})	ω (-)	AIC	ΔAIC	AIC weight
2	3	0.067	153		0.15	2009.6	0.0	0.66
4	4	0.067	138	174	0.15	2010.2	0.7	0.34
1	2		224		0.09	2248.1	238.5	0.00
3	3		198	255	0.09	2248.9	239.3	0.00

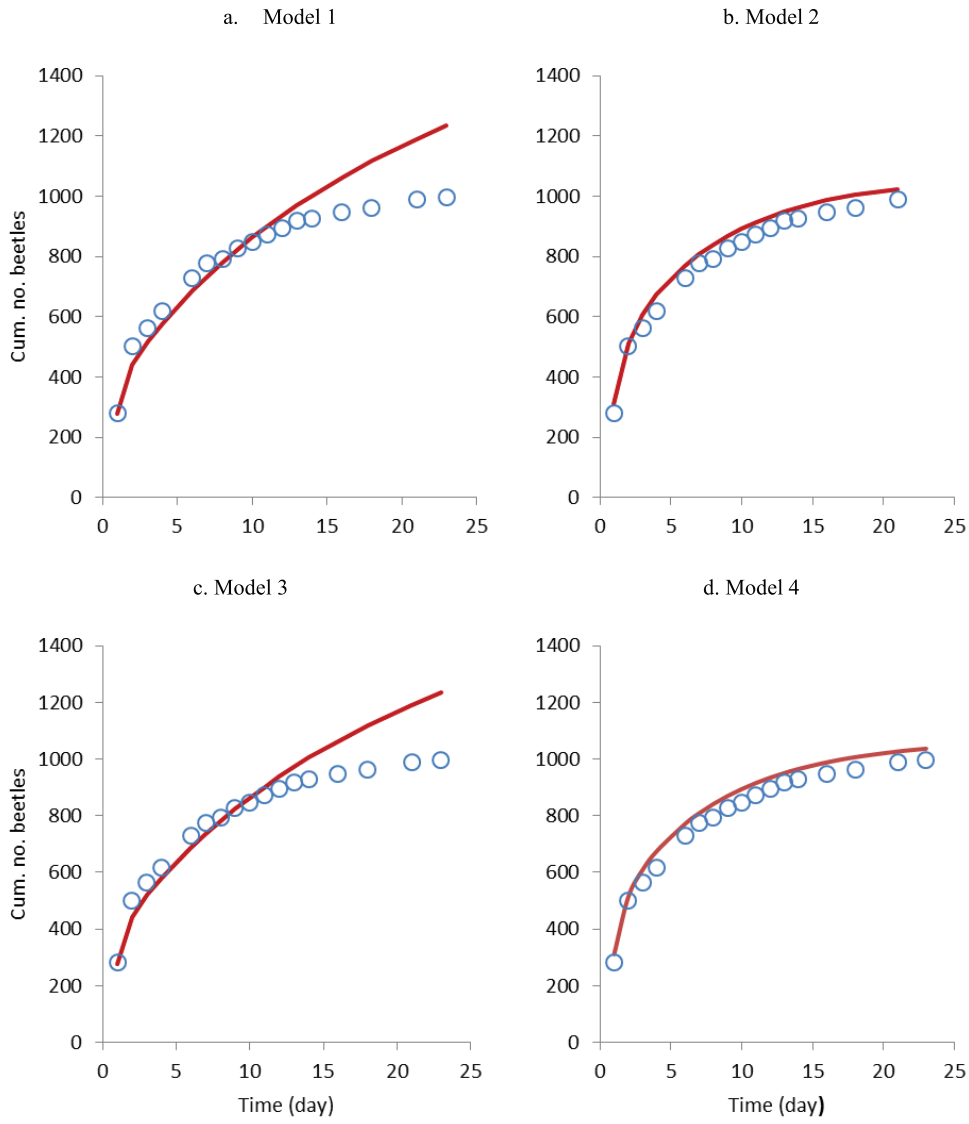

Figure 2. The cumulative number of beetles recaptured throughout the experiment (open circles) and the simulated number of recaptured beetles (solid lines) as estimated by 4 considered models with different diffusion constants (μ_1 and μ_2 for the two crops) and loss rate (ξ). (a) Model 1: $\mu_1 = \mu_2$ and $\xi = 0$; (b) model 2: $\mu_1 = \mu_2$ and $\xi \neq 0$; (c) model 3: $\mu_1 \neq \mu_2$ and $\xi = 0$; (d) model 4: $\mu_1 \neq \mu_2$ and $\xi \neq 0$.

ties over time within the experimental field. Yamamura *et al.* (2003) solved this problem by adding a loss term in the diffusion equation for removal due to trapping. Their solution, however, requires that traps are placed uniformly in a lattice pattern. As far as we know, our study is the first one to identify a dynamic movement model based on the Fokker-Planck equation from MRR data collected with an irregular grid of traps.

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